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The phenotypes of the Formica rufa complex in East Germany

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with 5 tables and 14 figures

Zusammenfassung

Die Phänotypen des *Formica rufa*-Komplexes in Ostdeutschland.

432 Nester des *Formica-rufa*-Komplexes (die Phänotypen nahe *rufa* L. und *polyctena* Förster) wurden auf dem Territorium von Ostdeutschland (DDR) in ihren Behaarungsmerkmalen, der Populationsgröße, der Monogyniefrequenz und anderen Merkmalen untersucht. Auf der Basis von Nestproben, die 7–20 Arbeiter pro Nest umfaßten, wurden 8 Behaarungsmerkmale und die Kopfbreite mit einer standardisierten Methode erfaßt, was 55 000 morphologische Primärdaten ergab. Drei eindeutige Behaarungsphänotypen **pht P**, **pht I** und **pht R** konnten nachgewiesen werden. Auf der Basis von Probenmittelwerten war es möglich, 427 Nester (= 98,8 %) einem dieser drei Hauptphänotypen zuzuweisen. Der Einfluß der Körpergröße auf die Behaarungsdaten kann bei Unterscheidungen zwischen **pht P** und **pht I** vernachlässigt werden, ist jedoch wichtig bei Entscheidungen zwischen **pht I** und **pht R**. Der intermediäre **pht I** wird als fertiler Hybrid zwischen den sympatrischen Subspezies *Formica rufa polyctena* (**pht P**) und *Formica rufa rufa* (**pht R**) gedeutet. Das wurde geschlossen aus den genau intermediären Positionen der Mittelwerte jedes der 8 Behaarungsmerkmale, aus der Tatsache, daß der Hybrid an den Orten häufiger war, wo beide Elternsubspezies gemeinsam vorkamen, aus der intermediären Größe der Populationen polygyner Nester und aus der intermediären Monogyniefrequenz. Der Hybrid ist weiterhin gekennzeichnet durch einen gravierenden Zusammenbruch der Korrelationen zwischen den Behaarungsmerkmalen (0,18 im Vergleich zu 0,49 bei **pht P** und 0,51 bei **pht R**). Zwei Beisiele für Nester mit ganz offensichtlichen Phänotypgemischen (**pht I** + **pht R**) und zwei Beispiele für vollzogene Übergänge von einem Phänotyp zum anderen (**pht P** verwandelt sich in **pht I**) werden beschrieben. Für eine sichere Bestimmung von Königinnen der drei Phänotypen sind Nestproben erforderlich. Die Methode von OTTO (1960) wird als sehr nützlich für die Unterscheidung von monogynen und polygynen Nestern bestätigt und mögliche Irrtumsfaktoren werden erörtert. Die ökologischen Strategien, die mit Monogynie und Polygynie verbunden sind, werden diskutiert. Die Monogyniefrequenzen erhöhen sich von **pht P** (2,4 %) über **pht I** (14,3 %) zu **pht R** (75,9 %). Es wird der Nachweis erbracht, daß sich die mittlere Körpergröße der Arbeiter mit wachsender Populationsgröße in monogynen Nestern erhöht, dagegen aber in polygynen Nestern geringer wird. Die Unterschiede der Phänotypen in der Häufigkeit der Infektion mit epizootischen Pilzen (**pht P** 23,2 %, **pht I** 15,7 %, **pht R** 2,6 %) werden durch unterschiedliche Koloniestrukturen und Dispersionsweisen der Ameisen und nicht durch unterschiedliche biochemische Eigenschaften der Cuticulaoberfläche erklärt. Der Hybrid **pht I** ist außerordentlich häufig (27,4% von 212 Nestern) in einem Gebiet der Oberlausitz mit einer zerrissenen, „grobkörnigen" Waldlandstruktur. Dagegen ist er selten (6,6 % von 218 Nestern) in Gebieten mit kompakten Waldlandsystemen, die eine niedrige Relation zwischen Randlinienlänge und Fläche aufweisen. Ein Modell über die Bildung sympatrischer Subspezies, das die geringe Häufigkeit von Hybridnestern in Regionen mit kompakten Waldlandsystemen und deren große Häufigkeit in zerrissenen Waldlandsystemen erklären kann, wird vorgestellt. Als taxonomische Benennungen werden vorgeschlagen *Formica rufa rufa* L., 1761 (**pht R**), *F. rufa polyctena* Förster, 1850 (**pht P**) und *F. r. rufa* x *polyctena* (**pht I**). Die geringe Häufigkeit von Proben zweifelhafter Phänotypzugehörigkeit legt es nahe, daß eine Selektion auf Stabilität der Hybridpopulationen existieren sollte.

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1. Introduction

The *Formica rufa* group, the mound-building wood ants of the Palaearctic, undoubtedly have always attracted the strongest interest of scientists, foresters and nature conservationists. The number of scientific publications dealing with these ants has reached a thousand or more. There has been much confusion in the taxonomy of this group before the taxonomic statements of YARROW (1955) and BETREM (1960) produced an order which was quickly adopted by a majority of myrmecologists and was often used in the sense of a dogma. However, the real situation in nature was not as simple as the established concepts of taxonomists demanded. Today, critical ant taxonomists are not sure whether we have 6 or 15 species of wood ants in Europe (COLLINGWOOD & AGOSTI 1986).

To throw light onto this matter, it seems adequate to make in the first instance a detailed study for a restricted geographical area giving a combined picture of morphology, mutual space partitioning and biological traits of the taxa in question. It is more easy to make a biological interpretation of the morphological entities by such a first step compared with a synopsis over large zoogeographical areas, which must be a more or less typological study because of the scattered and accidental supply with ant material and insufficient knowledge of local conditions.

This paper aims to elucidate the situation in the so-called *F.rufa* complex (as it was subdivided by COLLINGWOOD & AGOSTI 1986) for the restricted geographical area of NE Germany (the countries Sachsen, Sachsen-Anhalt, Thüringen, Brandenburg, Berlin and Mecklenburg-Vorpommern). According to the established concept, the only species from this complex present in NE Germany are *Formica rufa* Linnaeus, 1761 and *Formica polyctena* Förster, 1850. The wood ant taxa *pratensis, nigricans, truncorum* and *uralensis* are present but do not belong to the *F.rufa* complex.

55.000 primary data on morphology were incorporated in this study. The presented manuscript was basicly finished in autumn 1989 and thus produced under the bad technical conditions of the old economic system. This meant no access to and no experience in use of computing facilities. Ancient calculation systems had to be used which meant extreme expense of time and a constraint to ommit analyses not essential for the basic purpose of this treatise. However, the main pattern demonstrated below should hold when more complicated mathematical methods were applied and this paper provides a good evidence for the existence of three morpho-ecological entities within the German *Formica rufa* complex.

To prevent any taxonomic prejudice, I have restricted in the following text the use of the terminus "species" and the more neutral expression "phenotype" is applied. Phenotype P **(pht P)** is more or less that what is commonly understood as *"Formica polyctena"*, phenotype R **(pht R)** can be referred to *"Formica rufa"* and phenotype I **(pht I)** is an intermediate which attrected my special attention because it suggested a certain gene flow between the so called good species *polyctena* and *rufa*.

2. Material and methods of morphological investigations

The material for the study was collected in a territory delimited by 10°40'E to 15°E and 50°15'N to 54°35'N. A total of 432 wood ant nests were studied for worker morphology including 42 samples with queens. Males are not considered in this paper. The sample size of workers investigated for pilosity depended upon intranidal morphological variability; in cases of low variance, a sample of 7 workers per nest was regarded as sufficient but this was increased up to a maximum of 20 as variability increased and phenotype identy became unclear. For computation of OTTO's function or the demonstration of mixed nests, 30 to 170 workers were investigated.

In pilosity counts and measurements, only seta projecting more than 11 µm from cuticular surface were considered. Sometimes we have very few standing pubescence hairs which were not incorporated into the counts and are easily distinguished from seta or pilosity by their much smaller diameter of only 2–3 µm. The designation and location of body parts for pilosity counts follows DOUWES (1979) and I have restricted all pilosity numbers to one half of the body. However, there are often strong bilateral asymmetries in pilosity numbers and in the case of characters **uh, bh** and **pe,** both halves were counted and the number divided by 2. The vast majority of material was ethanol-stored which provides much advantage in seta counting but reduces the accuracy of metric measurements.

The following morphological characters were investigated:

HW = maximum head width in µm, measured slightly behind eyes in medium-sized or large workes and across eyes in very small workers.

uh = number of standing hairs on whole underside of head divided by two.

bh = number of standing hairs on whole occipital margin of head divided by two and seen in straight dorsal view.

pn = number of standing hairs on one half of pronotum; the conspicous but fine proprioreceptive sensillae at the anteriormost tip of pronotum are not counted while seta a little behind are included.

mn = the number of standing hairs on one half of mesonotum.

pp = the number of standing hairs on one half of propodeum.

pc = the number of standing hairs on whole margin of petiole scale divided by two.

uhl = length of longest hair on underside of head in µm.

pnl = length of longest hair on one half of pronotum in µm.

astl = length of longest hair on anterior half of underside of 1st gaster sternite.

pstl = length of longest hair on posterior half of underside of 1st gaster sternite.

st = number of hairs projecting more than 50 µm from underside of 1st gaster sternite as seen in lateral view.

All chactotaxy was performed in specimens with HW $\geqq$ 1400 µm because the size-dependent drop pilosity values is considerable in very small workers. The pilosity counts and head width measurements were performed at a magnification of 62x and hair length measurements at 125x under use of a TECHNIVAL 2 stereomicroscope (Jena).

3. Results of morphological investigations on workers

3.1. The initial hypothesis on phenotypes P, I and R with a simple pilosity index

We have a clear demonstration of at least three phenotypes computing a simple index of hairiness **H** from nest means as geometric mean of the five most discriminative characters. How these characters were sorted out is explained below. This crude index **H** is given by

$$\mathbf{H} = (\mathbf{uh} \times \mathbf{pn} \times \mathbf{pp} \times \mathbf{uhl} \times \mathbf{pnl})^{1/5}$$

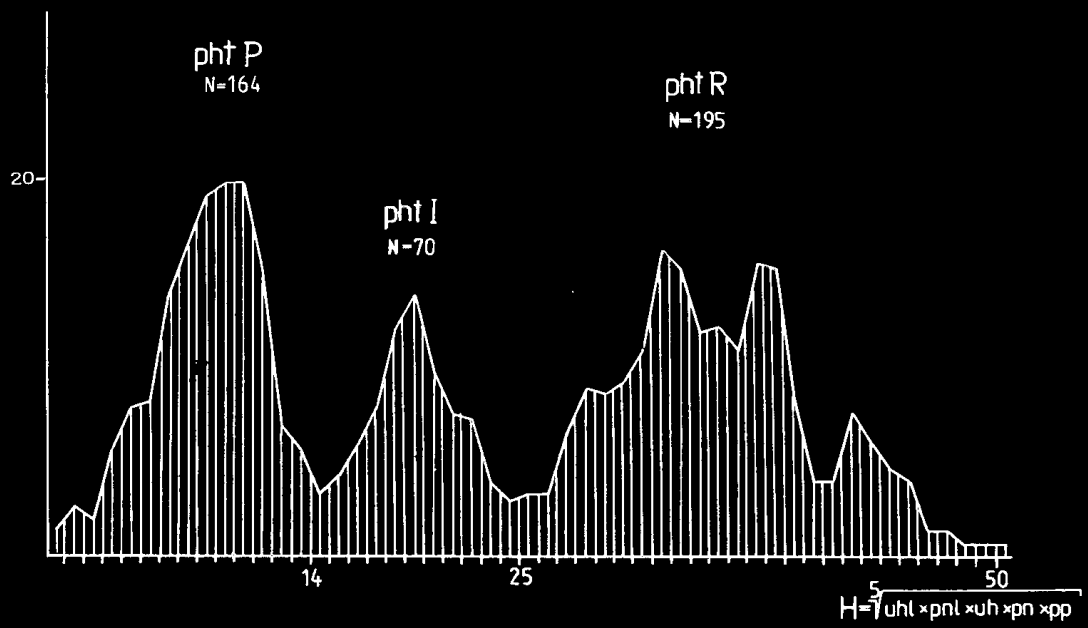


Fig. 1 Demonstration of pilosity phenotypes of the *Formica rufa* complex workers by a simple pilosity index **H** computed as geometric mean of the five most discriminative characters **uhl, pnl, uh, pn,** and **pp** which went into calculation as arithmetic nest means

Fig. 1 shows three well-separated peaks from which an initial hypothesis on phenotypes is derived with some confidence. 164 samples (= 38.2 %) belong to the first peak with H values of ≤ 14.5. These are designated as phenotype P **(pht P).** 16.3 % of all samples belong to the second peak within the interval $\mathbf{H} = (14.5, 25.0)$ and are designated as phenotype I **(pht I).** The remaining 45.5 % of samples with $\mathbf{H} > 25.0$ form together a broad third peak and are named phenotype R **(pht R).**

This third peak could possibly consist of three subentities but these are not clear enough to exclude possible artefacts. However, the putative existence of 5 instead of 3 entities is suggested and, remembering the biochemical investigations of GÖSSWALD & SCHMIDT (1959) who demonstrated in German material 5 different biochemical phenotypes for the wood ant group considered here, I am convinced that a separate analysis of the third entity would reveal a heterogeneous structure.

Let us consider now the characters one by one. The figures 2–9 show distributions of sample means for the characters **uh, bh, pn, mn, pp, pe, uhl** and **pnl** both in a non-discriminative pooled histogram of all samples as well as in a discriminating presentation of relative frequencies **p** ($\Sigma \mathbf{p}_i = 1.0$) for each phenotype. These relative phenotype frequencies were derived from the initial hypothesis. We observe a very different discriminatory power of characters. The discriminatory power **d** means the nonoverlap of frequency distributions between the three stated phenotypes with

$$\mathbf{d} = \frac{1}{2} \sum_{K=1}^{L} |\mathbf{P}_{AK} - \mathbf{P}_{BK}|$$

where **L** is the number of intervalls a character was subdivided in and $\mathbf{p}_{AK}$ and $\mathbf{p}_{BK}$ are

the relative frequencies (or probabilities with $\Sigma\, p_i = 1$) for phenotypes A and B. Table 1 gives a synopsis of all characters with arithmetic mean, borders of 95 % probability range, extreme values and discriminatory power on the basis of nest sample means. Arranged in falling order of discriminatory power the best characters are **pn, uhl, pp, pnl** and **uh,** having a non-overlap of 88–94 %, while **pe, mn** and **bh** are less useful with **d** ranging 47–78 %.

	phenotype P	phenotype I	phenotype R	dis. power
uh	0—0.15—**1.706**—3.5—4.1	2.3—2.4—**4.587**—6.6—6.7	3.7—4.9—**7.148**—9.9—10.45	0.8776
bh	0—0—**0.080**—0.34—0.7	0—0—**0.354**—0.97—1.38	0—0—**0.714**—2.3—3.83	0.4729
pn	0.25—0.4—**3.539**—8.25—11.0	5.0—5.9—**10.24**—14.6—16.7	11.9—15.3—**26.16**—39.9—46.9	0.9423
mn	0.70—1.0—**3.650**—6.80—8.25	2.3—2.6—**6.275**—9.94—10.8	3.9—5.3—**11.90**—19.4—22.9	0.7238
pp	0—0.2—**3.161**—6.90—8.31	4.6—4.7—**7.622**—10.65—11.5	8.0—9.5—**16.01**—23.5—28.6	0.9095
pe	0.3—0.8—**2.840**—5.20—6.30	2.22—2.9—**5.286**—7.6—8.0	3.21—5.3—**8.059**—11.5—12.9	0.7764
uhl	14—19—**57.6**—103—111	81—83—**125.5**—197—205	131—146—**192.7**—239—257	0.9110
pnl	5—8—**40.8**—62—66	52—53—**72.5**—97—103	76—79—**99.6**—123—135	0.8934
HW_{max}	1643—1686—**1831**—1998—2089	1658—1697—**1883**—2075—2220	1643—1770—**2001**—2193—2249	—

Table 1 Distribution of nest sample means of morphometric data in workers. Sequence of data for each character: lower extreme — lower limit of 95 % interval — **arithmetic mean** — upper limit of 95 % interval — upper extreme. The discriminatory power (= non-overlap of frequency distributions) was computed as arithmetic mean of the three between-phenotype values. HW_{max} is the largest head width in a nest sample.

3.2. The influence of body size on pilosity data and comments on confidence of phenotype determinations

Because of the limited computing capacity, I have confined all evaluations in this and the following sections on sample means. Such a reduction to 430 sample means is not expected to produce principally different results than a computation from 5500 individual workers. However, in detail, we may predict systematic deviations since the nest means were computed as arithmetic means in each character whereas tentative regressions with individual values, along a large body size range, frequently resulted in nonlinear functions, particularly in **pht R.**

Table 2 shows the dependency of pilosity data in the five most discriminating characters as function of HW. In general we can state the pilosity to be almost independent from body size in **pht P** and to have a weakly positive correlation in **pht I.** The rather low number of 164 or 70 regressed pairs in **pht P** or **pht I** does not allow to prove a significancy where a weak correlation really exists: In a tentative computation with 800 individual workers the reduction of **uhl** with growing HW in **pht P** was found to be highly significant ($p < 0.001$).

In **pht R** we have always a highly significant, positive correlation of pilosity length and number with body size. To have described the size-dependency of the pilosity index **H** and to reach a better phenotype separation, I have defined a size-corrected pilosity index $\mathbf{H}_{cor}$. Since slopes of regression lines increase the more hairy a phenotype is, it is appropriate to use different correction functions for either **pht P pht I** or **pht I pht R.** For $\mathbf{H} < 20.0$ the correction was

$$\mathbf{H}_{cor} = \mathbf{H} - 0.00253\ \mathbf{HW} + 4.23$$

and for $\mathbf{H} \geqq 20.0$ the correction was performed as

$$\mathbf{H}_{cor} = \mathbf{H} - 0.0101\ \mathbf{HW} + 17.0$$

where **HW** is given in μm. The slopes of these functions were estimated by regression of **H** against **HW** within the intervalls $\mathbf{H} = [11.0, 19.0]$ and $\mathbf{H} = [20.0, 30.0]$. The constants 4.23 and 17.0 were added to give $\mathbf{H}_{cor}$ similar values as **H.**

Fig. 11 shows the frequency distribution of $\mathbf{H}_{cor}$. Compared to Fig. 1, we have a better separation of **pht I** and **pht R** but no advantage to separate **pht I** and **pht P** indicating that only the correction function for $\mathbf{H} \geqq 20.0$ gives a sense. The largest $\mathbf{H}_{cor}$ for **pht I** is 23.8 and the smallest for **pht R** is 25.3 making one believe we have a perfect separation. However, we have to expect nest samples where in reality no either or decision is possible. This refers particularly to the rare nests with phenotype mixtures or to those rare nests where a shift from one phenotype to another is just in progress (see section 3.5). The same qualification must be made for distinction between **pht P** and **pht I.** For these reasons,

	phenotype P (n = 164)					phenotype I (n = 70)					phenotype R (n = 195)				
	F	G	p	$Y_{1.6}$	$Y_{1.9}$	F	G	p	$Y_{1.6}$	$Y_{1.9}$	F	G	p	$Y_{1.6}$	$Y_{1.9}$
uh	— 0.686	2.98	n. s.	1.9	1.7	2.414	0.42	.05	4.3	5.0	4.453	— 1.16	.001	6.0	7.3
pn	— 0.217	4.27	n. s.	3.9	3.9	— 3.597	16.36	n. s.	10.6	9.5	26.48	—22.0	.001	20.4	28.3
pp	— 2.244	6.92	n. s.	3.3	2.7	1.599	4.94	n. s.	7.5	8.0	15.59	—12.57	.001	12.4	17.0
uhl	—30.90	108.2	n. s.	59	49	106.3	—61.0	.001	109	141	99.69	10.33	.001	170	200
pnl	— 0.643	41.7	n. s.	41	40	17.98	42.5	n. s.	71	77	34.98	35.15	.001	91	102
H	— 0.809	9.76	n.s.	8.5	8.2	5.91	9.80	.05	19.3	21.0	25.02	—10.57	.001	29.5	37.0

Table 2 Dependency of pilosity data from head width HW of worker ants described as linear function of the type $Y = F\,x + G$; x is head width in mm, p is the significancy level of regression line, $Y_{1.6}$ and $Y_{1.9}$ are predicted pilosity data for head widths of 1.6 and 1.9 mm. The regressions were computed on the basis of sample means.

the percentage of possible misidentifications with the initial phenotype determination (**pht P**: $H \leqq 14.5$, **pht I**: $H = [14.5, 25.0]$, **pht R**: $H > 25.0$) or the size-corrected index (**pht I**: $H_{cor} \leqq 24.5$, **pht R**: $H_{cor} > 24.5$) is difficult to assess. However, we can approximate the problem by a description of the histograms in Fig. 1 and Fig. 11 with three superimposed normal curves and a calculation of the corresponding confidence limits. For Fig. 1, the 95 % confidence limits are $H = [2.9, 14.2]$, $H = [14.8, 24.5]$ and $H = [25.3, 45.7]$ for the first, second and third peak. The normal curves predict only 2.0 % of the first entity to have values > 14.5 and only 1.9 % of the second entity should have values $\leqq 14.5$. Only 1.5 % of the second normal curve is found above 25.0 and 2.2 % of the third normal curve below 25.0. These data mean an overall frequency of probable misidentifications of 1.9 % or 8 nests samples in a total of 430 (in this calculation are not included two nest samples with extreme phenotype mixtures, see section 3.4).

For the size-corrected index H_{cor} we get no good fit with three normal curves and confidence intervals can not be calculated but this does not weaken the better separation this index generates between **pht I** and **pht R.** In distinction between **pht P** and **pht I** we have to expect misidentified samples for $H = [13.5, 15.5]$; these are 5 samples in our material:

sample No.	289	351	41	428	100
index H	13.5	14.0	14.5	14.7	14.9
designation	**pht P**	**pht P**	**pht P**	**pht I**	**pht I**
designation real?	o.k.	o.k.	unclear	unclear	likely

Sample No. 289 and 351 were collected in two large, compact woodlands with dense polycalic populations of **pht P** at the collecting site, no **pht I** nests were observed in the neighbourhood or in the whole forest and it is very unlikely that these samples could be another phenotype. Nest No. 100 was found in a forest with syntopic occurrence of all three phenotypes but an extremely high abundancce of **pht I.** It is most likely a lower pilosity extreme of **pht I.** In samples No. 41 and 428 colony structure, habitat or chorological situation do not provide suggestions on phenotype identity. To summarize, a good knowledge of the situation in and around the nest site should enable the interpretation of a certain portion of the 1.9 % of possibly misidentified samples and to reduce the number of unclear samples to 0.7 % (or 1.2 % including the mixed samples).

3.3. The breakdown of correlations between pilosity characters and a morphological argument for hybrid identity of phenotype I

Except of **bh** which has a large relative error and is of restricted use for phenotype separation, the correlations between the pilosity characters are shown in the matrices below.

pht P (from 164 sample means)

	pn	mn	pp	pe	uhl	pnl
uh	0.3928	0.4002	0.3969	0.3982	0.8030	0.2500
pn	—	0.6131	0.6336	0.5215	0.2455	0.6473
mn			0.6643	0.5204	0.3465	0.5110
pp				0.6737	0.3818	0.5862
pe				—	0.3882	0.4463
uhl					—	0.4246

mean 0.4879 ± 0.1475 (n = 21)

pht I (from 70 samle means)

	pn	mn	pp	pe	uhl	pnl
uh	0.2636	0.2359	0.1056	0.0283	0.4299	−0.1951
pn	—	0.3980	0.3707	0.0840	0.1053	0.2627
mn			0.3798	0.2046	−0.2317	−0.1043
pp				0.3805	0.2203	0.1737
pe					0.0995	0.1661
uhl						0.4510

mean 0.1825 ± 0.1949 (n = 21)

pht R (from 195 sample means)

	pn	mn	pp	pe	uhl	pnl
uh	0.6089	0.5250	0.3764	0.3260	0.5251	0.5412
pn	-	0.7555	0.7022	0.5597	0.4776	0.6121
mn		—	0.6660	0.5321	0.3997	0.4318
pp			—	0.6841	0.3424	0.4322
pe				—	0.2762	0.3783
uhl					-	0.5870

mean 0.5114 ± 0.1341 (n = 21)

The correlations printed in heavy type are significant at the $p < 0.01$ level. We observe a highly significant breakdown of correlations in **pht I** compared to **pht P** and **pht R.** This is an exciting phenomenon which can not be explained as an artefact of erroneous phenotype determination: a false allocation of **pht P** or **pht R** samples to **pht I** would in both cases raise the correlations in the **pht I** matrix and, on the other hand, a false allocation of **pht I** samples to **pht P** or **pht R** would not reduce the correlations in the **pht P** and **pht R** matrices.

A biological explanation of this phenomenon could be that **pht R** and **pht P** have lived in *de facto* reproductive isolation for longer periods in the past when there was a natural, compact woodland structure in Central Europe which reduced the chance of encounters of the two phenotypes (see sections 5.2, 6 and 10). This lead to genetical divergence. With the drastic change of woodland distribution and structure after the large clearfellings in the beginning of this millenium, the reproductive isolation was broken and hybrids still fertile and with sufficient fitness occurred. However, a reduced fitting-together between certain gene products seems possible. Such an affection of harmonizzing within multiple gene systems should be tolerated as far as only peripheral phenes which do not have a notable influence on fitness and no fundamental functional systems are affected. Thus a possible hybrid origin could explain the breakdown of correlations between pilosity characters in **pht I.**

Intranidal variability of pilosity data could indicate genetic heterogenity which should be larger in a hybrid population. In analysing intranidal variability we encounter several problems which make comparisons between the phenotypes very difficult:

(i) the frequency of polygyneous nests differs (97.6 % in **pht P,** 85.5 % in **pht I,** 24.1 % in **pht R**),

(ii) concluded from nest size differences, the average queen numbers in polygyneous nests differ (**pht P^P > pht I^P > pht R^P**),

(iii) the pilosity data are not normal distributed but positively skewed in case of very low nest means,

(iv) within a phenotype, the standard deviation of pilosity data increases more slowly than the nest mean (see Fig. 12) – i. e. the ratio SD/mean decreases with increasing means.

These problems could be avoided or diminished if the comparisons are restricted to monogyneous samples which have similar nest means of pilosity. For a test between **pht I** and **pht R** and the characters **pn** and **pp** I have considered only samples in the interval **pn** [9.7, 17.4] and **pp** [7.2, 12.3] where problem (iii) is absent and problem (iv) has no importance. Seven monogyneous samples of **pht I** with **pn** [9.7, 14.6] had standard deviations of **pn** (SD_{pn}) of 3.5, 3.7, 4.1, 6.2, 6.4, 6.8, 11.6 and eight monogyneous samples of **pht R** with **pn** [11.3, 17.4] had SD_{pn} of 1.9, 2.0, 2.3, 2.7, 2.7, 3.9, 3.9, 6.3. Seven samples of **pht I** with **pp** [7.2, 11.9] had SD_{pp} of 2.8, 3.0, 3.0, 3.85, 5.5, 5.64, 6.0 and 17 samples of **pht R** had SD_{pp} of 1.1, 1.4, 1.8, 2.2, 2.23, 2.3, 2.3, 2.4, 2.5, 2.5, 2.83, 3.55, 3.6, 3.6, 3.95, 4.1. According

to a unidirectional MANN-WHITNEY test (U test), the SD_{pn} of **pht P** are significantly smaller than in **pht I** for $\alpha = 0.025$ while the SD_{pp} are significantly smaller for $\alpha = 0.005$. This is evidence that monogyneous **pht I** nests have a higher intranidal variability than **pht R** nests of equal colony status. A similar test for **pht P** **pht I** is impossible because of the lack of comparable monogyneous **pht P** samples.

The above interpretation of character correlations and intranidal variability is surely somewhat speculative but a much better argument for possible hybrid origin of **pht I** provide the positions of mean values of all pilosity characters studied (see Table 1). In hair length data as well as in square-root-transformed pilosity numbers, the mean of **each** character of **pht I** is almost exactly equal to the median position between the means of the putative parent entities **pht P** and **pht R.** The correlation between the 8 **pht I** means and these median positions is $r = 0.9999$ which is intriquing.

3.4. Intranidal phenotype mixtures, phenotype shifts and eventual linkage of the phenotypes

It is difficult to estimate the ratio of nests containing a phenotype mixture because the within-phenotype variability is considerable even in nests with regular pilosity distributions which are not suspected to contain mixtures. Data from such normal nests are summarized in the following table.

H interval	[0.0, 14.5]	[14.5, 25.0]	[25.0, 65.0]
pht P (614 workers from 62 nests)	80.7 %	18.0 %	1.3 %
pht I (847 workers from 67 nests)	25.0 %	55.6 %	19.4 %
pht R (360 workers from 42 nests)	0.8 %	13.1 %	86.1 %

Considering the summed intranidal standard deviation of pilosity numbers $SD_6 = SD_{nh} + SD_{bh} + SD_{pn} + SD_{mn} + SD_{pp} + SD_{pr}$, we have 430 samples with $SD_6 \leq 26.6$. From these samples it is difficult to sort out undoubtedly mixed nests. However, two another nest samples which data were not incorporated into Figs. 1–12, Tables 1–2 and other comparative statistics showed a very clear phenotype mixture: nest No 43 with $SD_6 = 32.9$ and a mean hair sum $S_6 = 44.9$ and sample and nest No 454 with $SD_6 = 45.3$ and $S_6 = 66.3$. Nest No 43 was a small oligogyneous colony at the site Liebsteiner Berg near Görlitz and contained in 1984 workers from nearly bare **pht P** (hair sum = 8) to extremely hairy **pht R** workers (hair sum up to 116). In the same year I removed two functional queens from this nest; one of these showed characters suggesting a **pht R** or **pht I** queen and the second had characters of a **pht R** queen. Two years later the nest was still in a good condition or even a little more populous but the extremely hairy worker fraction (offspring of the one removed hairy **pht R** queen?) had disappeared and SD_6 had fallen to a normal value of 19. 8.

The site Liebsteiner Berg is a small woodland of 8 ha in which I found as much as 24 **pht I** nests (20 **Ip** (= polyneous) + 4 **Im** (= monogyneous) nests) and 10 **pht R** nests (4 **Rp** + 6 **Rm** nests). This very close spatial neighbourhood means a high frequency of possible between-phenotype encounters. In case of nest No 43, a plausible interpretation seems to me that is was originally a 'pure' **Ip** nest which had accepted a **pht R** queen. I had the impression that, at this site, the **Ip** nests contained more frequently a small fraction of **pht R** workers than observed for **Ip** nests in other sites with less close contacts of both phenotypes. The acceptance behaviour of **Ip** nests to freshly dealate queens was observed here several times. As a rule, queens of own phenotype (from alien or own nest) as well as **pht R** queens were attacked and the majority was obviously killed but these attacks were sometimes less vehement or lacking. Nests producing both males and queens were not very rare in **pht Ip** and intranidal mating is probably no exception in such nests. Even in nests not producing queens, the males showed intensive mating behaviour already on mound surface, mounting workers or individuals of own sex. If **Ip** males performed a nuptial flight, it seemed, for most individuals, short-ranged and not directed to very distant targets, in so far as tracking of flight movements was possible in this woodland.

Few observations of **Rm** nests confirm the conventional thesis that any dealate queen is killed by fierce attack. However, such a schedule cannot be an invariable trait of all

R^m nests – otherwise a shift from monogyny to polygyny would be impossible. The adoption behaviour of **pht** I^m is unknown to me.

As for acceptance behaviour in polygyneous nests, it seems reasonable to conclude from different average population numbers (see section 8.) on a declining readiness to adopt queens from **pht** P^P across **pht** I^P to **pht** R^P.

At this point, I want to present a hypothesis on a possible correlation between external morphology of queens and queen/colony behaviour which could be more or less valid for all phenotypes considered here. The most critical point of this hypothesis is that the distinction of the two queen morphs is not free of subjectivity and I have no statistical evidence for a bimodality. These morphs are defined as opposite extremes to express more clearly what I want to say which does not mean intermediates are lacking:

	queen morph P	**queen morph M**
morphology:		
head width	$< 2050\ \mu m$	$> 2150\ \mu m$
center of scutellum	longitudinally striate	shining
dorsal gaster surface	less shining	brilliantly shining
gaster size	less voluminous	voluminous
found ratio of queens		
in **pht P**	96 % (n = 49)	4 % (n = 2)
in **pht I**	76 % (n = 37)	24 % (n = 12)
in **pht R**	46 % (n = 21)	54 % (n = 25)
ascribed functional characters		
dispersal flight:	absent or short-ranged	long-ranged
ability for socialparasitic colony foundation in Serviformica:	low	high
egg laying capacity:	low	high
queen effect on workers:	low	high

The queen effect means here the probable influence of queen secretions on worker aggressivity towards alien queens. The ratios of queen morph P correlate with the observed polygyny frequencies. This is an argument to put forward the hypothesis that the statistic differences of the phenotypes in dispersal capacity, colony foundation and structure (see sections 5.2 and 6) could be the result of statistic differences in morpho-ethological queen types.

Of particular interest is the mixed nest No 454 from Deutsch-Paulsdorf near Görlitz. On 19 March 1989 it contained worker phenotypes with such extreme pilosity differences that each individual was easy to allocate either to **pht I** or **pht R**. The sample contained

83 workers with $H_{cor} = 19.7 \pm 6.48$ [5.2, 32.0] and
109 workers with $H_{cor} = 42.6 \pm 2.99$ [35.5, 50.5].

The head width distribution indicated for each phenotype a highly significant monogyny; the OTTO discriminant was $L = 194.8$ for the **pht I** fraction and $L = 207.8$ for the **pht R** fraction. A sample taken in March 1990 contained 94 **pht I** and 107 **pht R** workers which is an almost unchanged ratio. This unexpected result contradicts the interpretation that an adoption of a **pht R** queen by an orphaned **pht I** colony (or vica versa) has taken place and suggests both fractions to be the offspring of the same queen. A long-term observation of this colony will possibly bring more clarity.

A representative statement on the real frequencies of phenotype shifts is not possible from my data since only 38 nests out of 432 were reinvestigated a few years after the first study. In these 38 nests, I have only one clear example for a phenotype shift from the site Spitzberg near Deutsch-Paulsdorf: This mound, a good-sized polygyneous colony, contained **pht P** workers with $H_{cor} = 10.4$ (sample No 64) in the year 1984 but it had definitely shifted to **pht I** with $H_{cor} = 21.4$ (sample No 441) in the year 1988. I found 5 **pht P**, 6 **pht I** and 3 **pht R** nests in this site in 1988 and most likely the shift was performed through repeated acceptance of **pht I** (or **pht R**) queens from neighboured colonies and gradual displacement of resident **pht P** queens. In this context a sentence of GÖSSWALD (1981) is interesting. He wrote that queens of his intermediate "Form II" will displace queens of *„Formica polyctena"* because "Form II" queens were "duftlich dominant" and

were preferred by *polyctena* workers. What GÖSSWALD understood as "Form II" is not sure because he gave only diffuse verbal descriptions on morphology which were as vague as his morphological descriptions of his "Mittlere Rote Waldameise" *Formica rufa rufopratensis major* GÖSSWALD, 1941 of which we have no types. However, from the complex life picture outlined by GÖSSWALD it is very probable that "Form II", the "Mittlere Rote Waldameise" and the intermediate **pht I** in my designation refer to the same morpho-ecological entity.

My investigations on material from the Soviet Union are not considerd here but one striking example for a phenotype shift should be mentioned. Near Svenigorod, 50 km W of Moscow, Dr. G. DLUSSKY showed me two proximate, good-sized wood ant mounds. The one nest (sample No 167) was a clear **pht I^P** nest (H_{cor} = 22.6) and the other nest (sample No 168) a clear **pht P^P** nest (H_{cor} = 6.2). According to DLUSSKY's long-term observations, the **pht I^P** nest was a daughter nest of the **pht P^P** nest. As in the Spitzberg colony, a possible explanation could be that the daughter nest had repeatedly accepted queens of hairier phenotypes which displaced the **pht P** queens. I recorded 5 **pht P**, 8 **pht I** and 2 **pht R** nests at the site Svenigorod which makes such an interpretation plausible. The Spitzberg and the Svenigorod case suggest that we probably have something like a "multiple social parasitism" of dominant hairier queens in less hairier host nests.

4. Morphological investigations on queens

A sufficiently safe phenotype determination of queens is not possible in single, isolated specimens but requires a nest sample because within-phenotype and within-nest variability is large. This refers particularly to microsculpture of scutellum and first gaster tergite which are unfortunately often quoted as key characters to separate *F. polyctena* and *F. rufa* (KUTTER 1977, COLLINGWOOD 1979). I found in **pht R** nests, among 56 studied queens, 7 (= 12 %) specimens which would have been determined as "clear" *polyctena* due to microsculpture and surface characters and, on the other hand, two queens among 23 **pht P** queens with "clear" *rufa* surface characters. The situation in **pht I** is still more heterogeneous and produces a lot of confusion. Further, such characters are difficult to quantify and it is often a matter of individual taste whether a surface is regarded as shining or dull, finely striate or smooth.

In pilosity characters we have significant differences of the means but again considerable overlap. The following table shows head width and pilosity data of first gaster sternite and is based on 34 nest samples with 145 queens. Only queens taken directly from the nests were incorporated to have a sufficiently safe phenotype determination:

	pht P (n = 56)		**pht I** (n = 57)		**pht R** (n = 71)	
	mean SD	range	mean SD	range	mean SD	range
HW	2013 ± 67	[1879, 2166]	2118 ± 66	[1944, 2317]	2140 ± 63	[2027, 2271]
pstl	189 ± 107	[24, 379]	307 ± 81	[27, 407]	375 ± 38	[180, 423]
astl	34 ± 10	[0, 62]	66 ± 49	[19, 274]	185 ± 76	[27, 302]
st	2.61 ± 2.00	[0, 6]	7.73 ± 4.84	[0, 25]	22.24 ± 7.78	[3, 41]

The large overlap ranges in the table above show queens are not easier to separate than workers. Comparably to the situation in workers, we may have nests with phenotype mixtures as for example in **pht R** nest No 26:

queen No	HW	pstl	astl	st
1	2229	388	209	24
2	2128	372	216	21
3	2113	180(!)	27(!)	3(!)
4	2182	316	268	19
5	2109	407	206	19

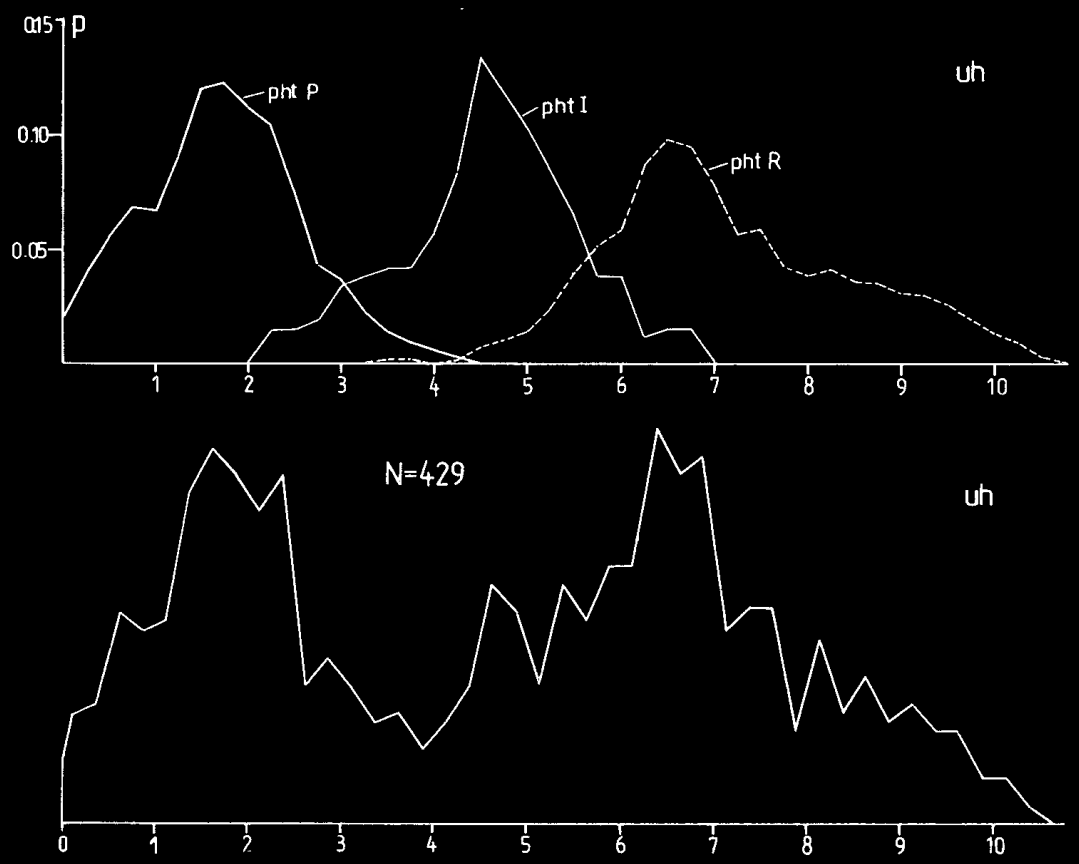
5. Monogyny and polygyny

5.1. The methods to distinguish between monogyny and polygyny

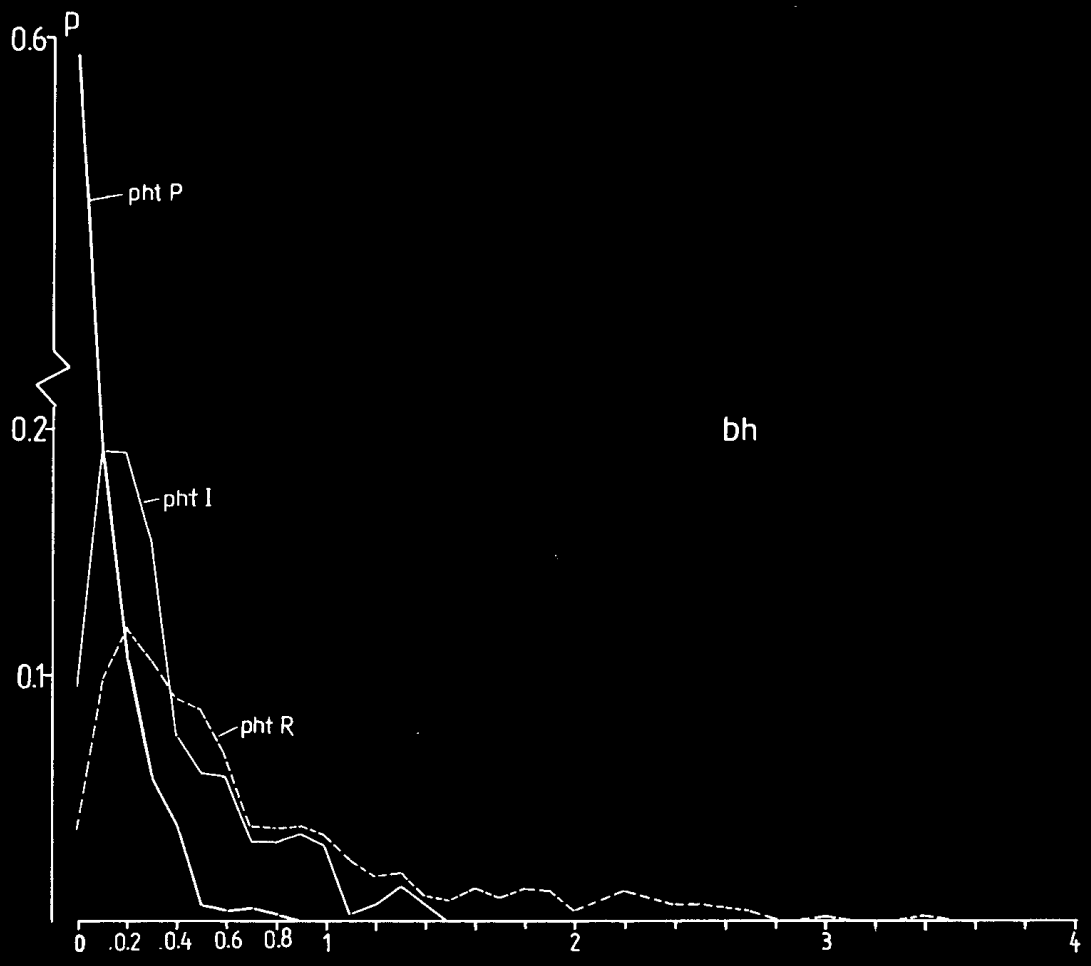
It was possible to assess the colony type immediately at the nest site in the majority of investigated wood ant nests. Such a field determination is facilitated by the fact that worker body size increases with growing size of nest populations in monogyneous colonies but decreases the larger the population number is in polygyneous colonies (see section 5.2, Fig. 14). Polydomous colonies are nearly always polygyneous although monogyneous colonies may consist of two or three separated mounds for shorter periods of time when the nest site is shifted.

If the site can not be observed for a reasonably long period and population or worker size are not sufficiently large to indicate the queen number, a test with OTTO's function is necessary. OTTO (1960) developed a method to discriminate between monogyneous and polygyneous colonies by a discriminant function the variables of which were obtained from head width measurements in 50 to 100 workers/nest. He noted that monogyneous colonies characteristically showed a clearly skewed distribution with a steep, high peak at large head widths. In contrast, polygyneous colonies have symmetric, flatter frequency distributions with the highest frequencies near the mean or sometimes they have a broad bimodal symmetry. In the OTTO function we have three variables. The first is mean head width **X** of the sample given in units of 10 µm. The second is the skewness measure **S** with

$$S = \frac{\Sigma\, p_i\,(x_i - X^3)}{n\, s^3}$$



Figs. 2–9 (continued overleaf) Frequency distribution of 429 sample means of different pilosity characters of workers both in a non-discriminated pooled histogram as well as in a discriminated presentation of relative frequencies **p** ($\Sigma p_i = 1$) for each phenotype. These relative frequencies were derived from the initial hypothesis. Data of two nests with clear phenotype mixtures are not incorporated.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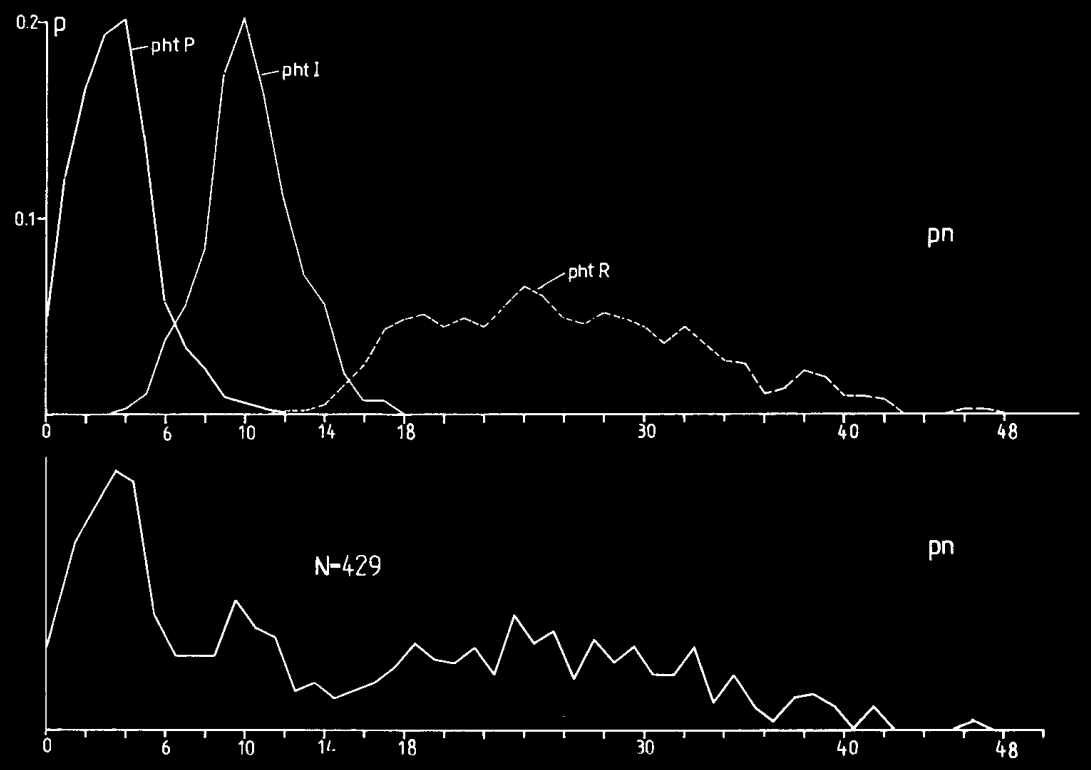
P
pht P
0.2
bh
pht I
0.1
pht R
0
.0.2
.0.4
0.6
0.8
1
2
3
4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pht P
pht I
0.1
pn
pht R
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10
14
18
30
40
48
N-429
pn
0
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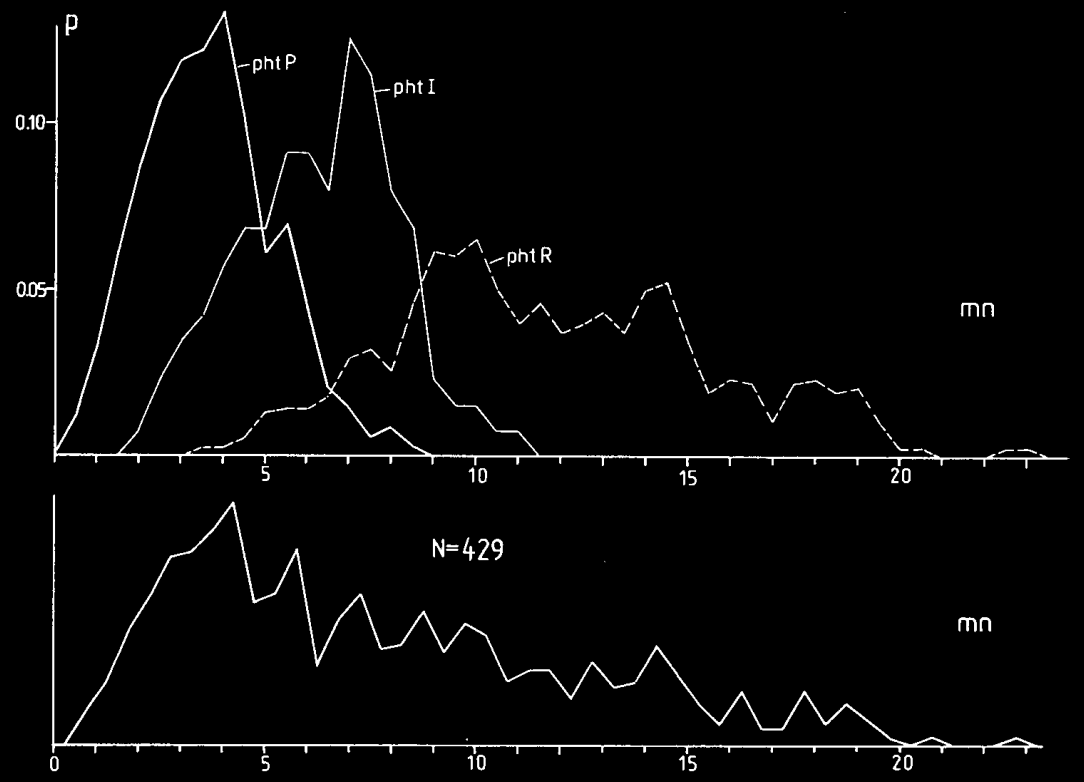
10
18
30
40
48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phtI
phtR
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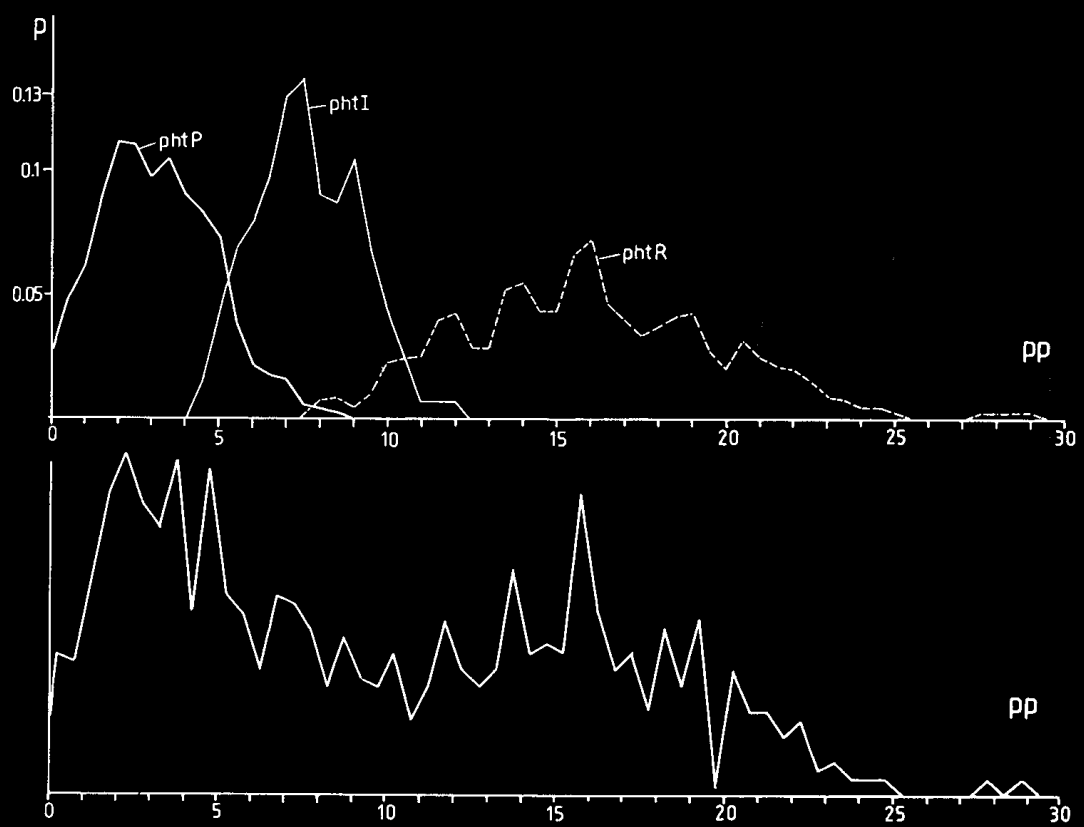
mn
5
10
15
20
N=429
mn
0
5
10
15
20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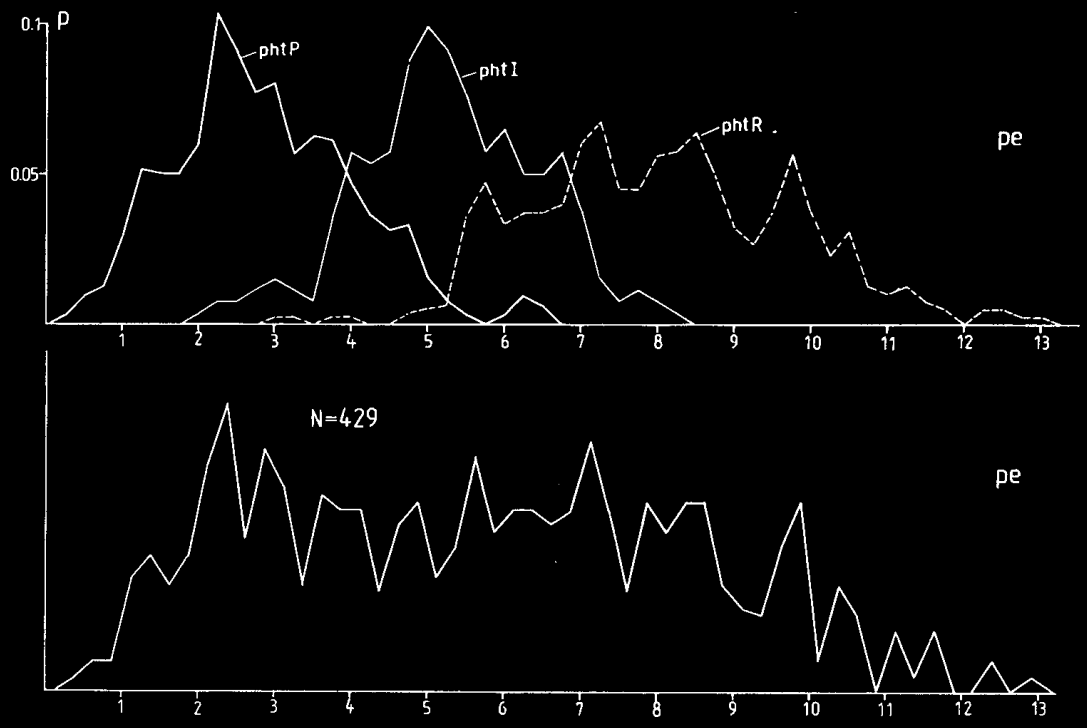
0.1
0.05
phtI
phtP
phtR
pp
0
5
10
15
20
25
30
pp
0
5
10
15
20
25
30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0.05
phtP
phtI
phtR
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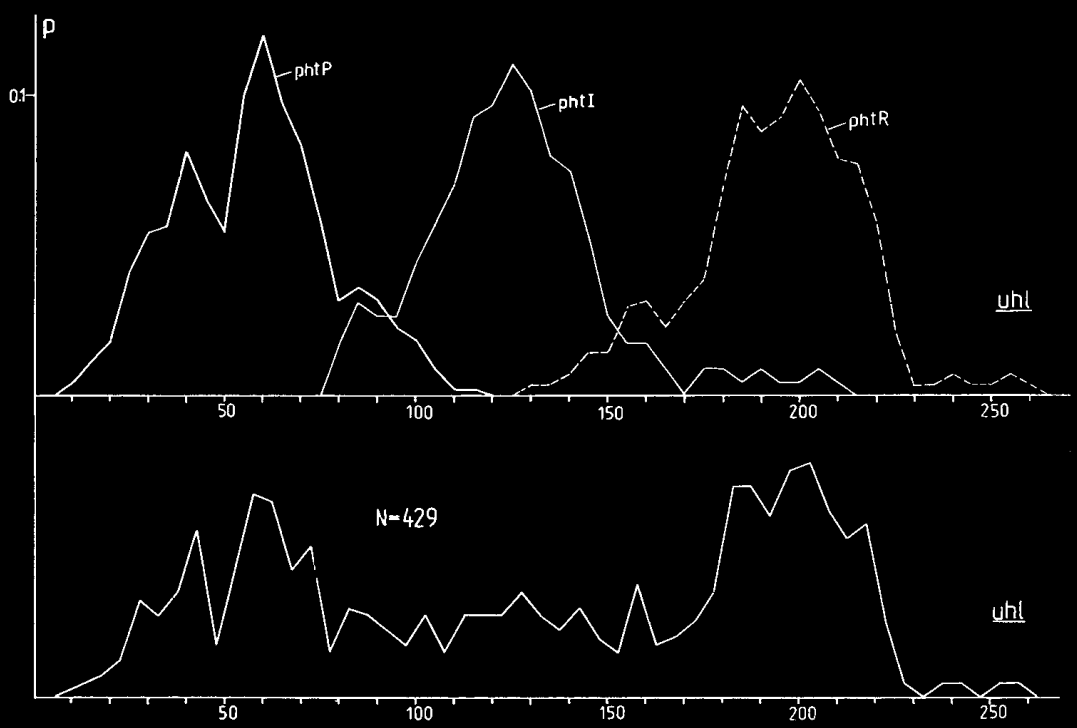
1
2
3
4
5
6
7
8
9
10
11
12
13
N=429
pe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phtP
phtI
phtR
uhl
50
100
150
200
250
N=429
uhl

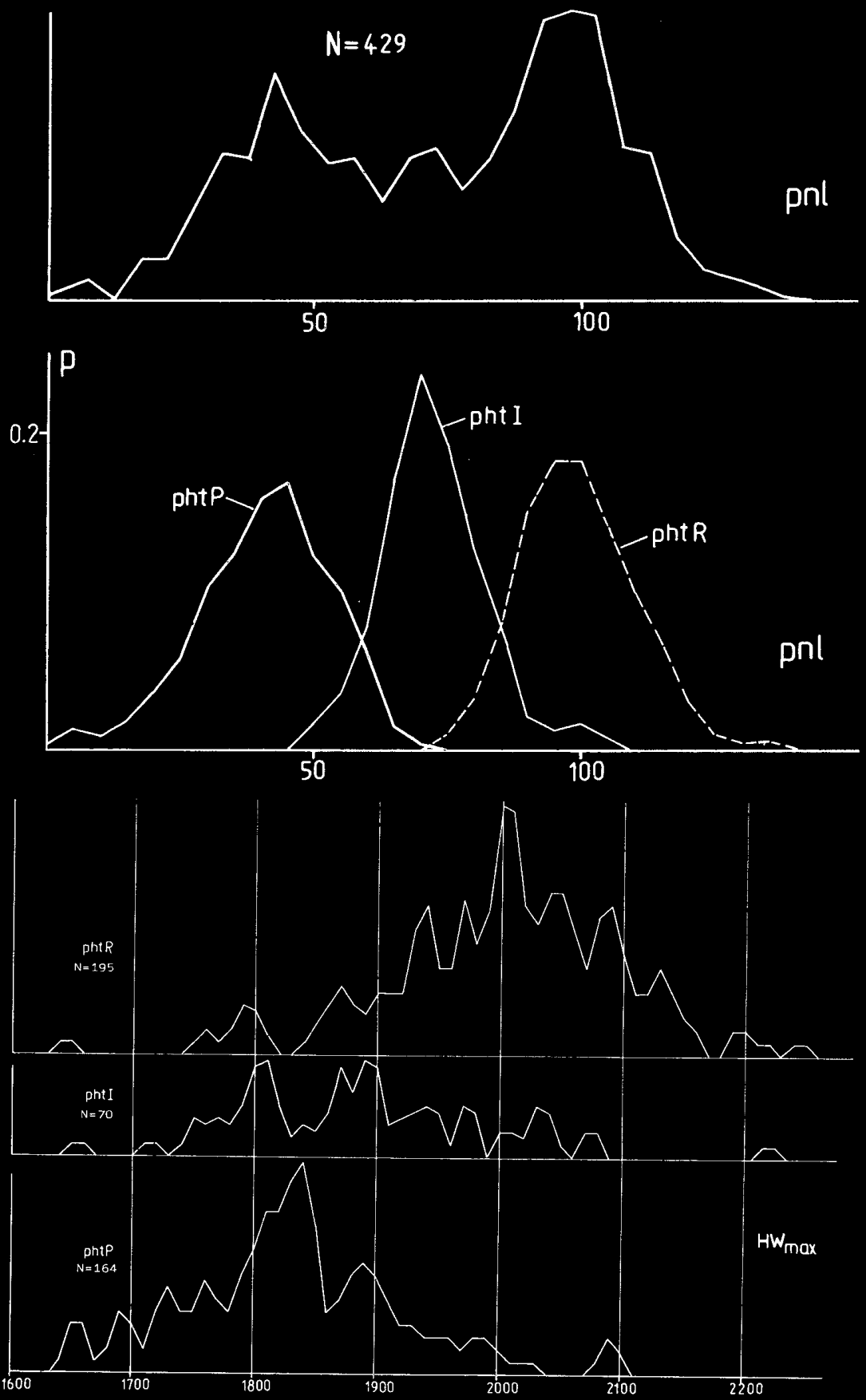

Fig. 10 Frequency distribution of the maximum within-sample head width HW_{max} of workers of the three phenotypes

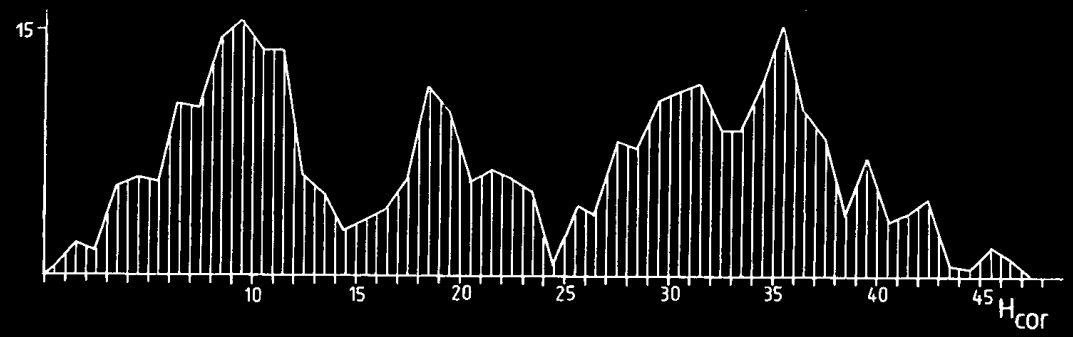

Fig. 11 Frequency distribution of the size-corrected pilosity index H_{cor} computed from pilosity index H (see Fig. 1) and a correction function with head width (see section 3.2.)

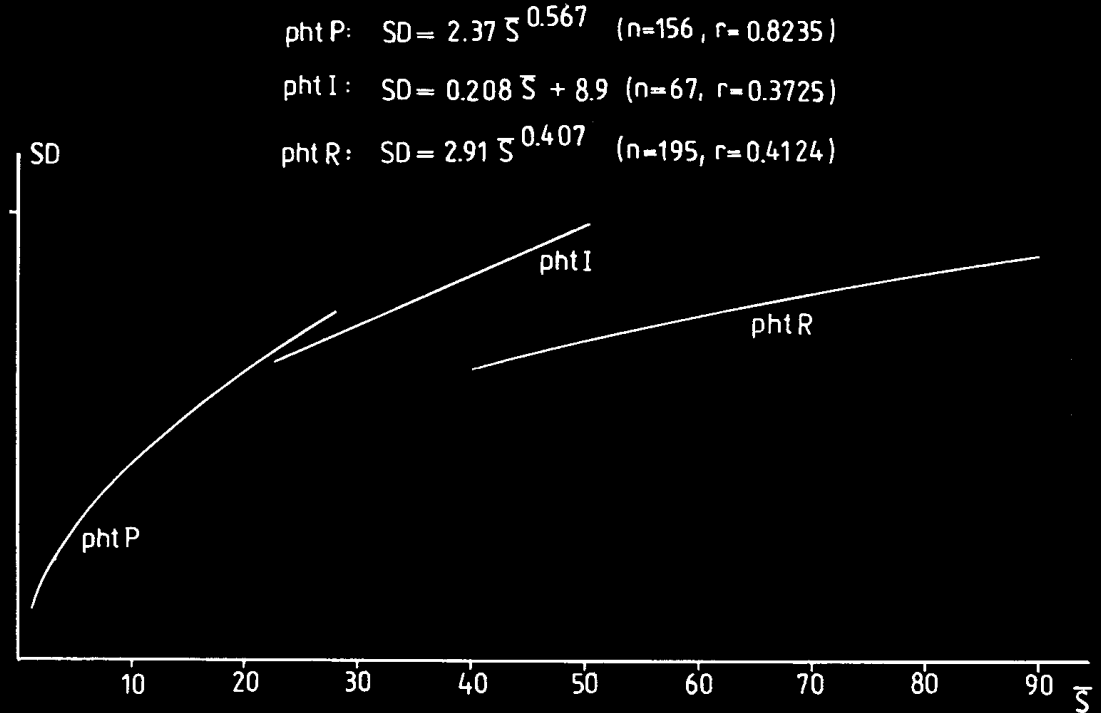

Fig. 12 Dependency of intranidal variation from pilosity number. The intranidal standard deviations of the characters **uh, bh, pn, mn, pp,** and **pe** were summed up to give **SD** and itranidal means of these characters were summed up to give **S**.

where p_i is the probability for a certain head width x_i, **n** the sample size and **s** the standard deviation. The third variable is the kurtosis (in German *Exzess)* measure **E** with

$$E = \frac{\Sigma\, p_i\,(x_i - X)^4}{n\, s^4} - 3.$$

The discriminant value **L** is then computed as

$$L = X - 16.66\, S - 1.92\, E.$$

OTTO found nests with $L < 180$ as safely monogyneous and those with $L > 186$ were safely monogyneous.

In principle I can confirm OTTO's function as very useful method and, despite it has some sources of error, it does not deserve to be forgotten. My results are as follows:

About 80 % of investigated nests were determinable as mono- or polygyneous already in the field either from their very large workers and skewed body size distribution, from their numerous worker population or from direct observation of queens on mound surface in early spring. For reasons of the threatened status of wood ants, digging out was done in four nests only. In 103 nests, including a portion of nests with clear queen status, the OTTO function was calculated. I got **L** values between 128 and 184.6 for 67 polygyneous nests and such between 184.9 and 217 for 34 monogyneous nests. OTTO's results were similar but, weakly deviating from OTTO, I have *empirically* shifted the uncertain interval about two units to larger values with $L = [182, 187.6]$. The reason for this weak deviation is not known. Apart from possible adjustment errors of measuring devices, I can not exclude to have made a small subjective error in sampling; many of the samples were taken with a pincers at the outer nest margin which could have meant that larger workers were a little overrepresented because they attracted more attention of the collector's eye or because their recruitment rate for enemy defense towards the sampling spot was higher than in small workers. Thus behaviour of ants and collector as well could have produced a weakly biased sampling. Nevertheless, the results are satisfying. I got only 7 samples within uncertainty range of **L** meaning 2.1 % of undetermined samples. Fig. 13 shows the distribution of **L** values within the interval $L = [160, 205]$.

However, this prima facie splendid determination rate of 98 % does not mean that certain sources of error need not be considered cautiously. At first, unclear results or even misidentifications with the OTTO function are to be expected one year or later after a shift from monogyny to polygyny. Nest No 46, a **pht I** nest, was a small colony with large workers and a clearly monogyneous body size distribution in the year 1984. At the second control of this nest in spring 1986, I noted an increase in population size ($A = 10$, see section 8.) and enlarged ratio of smaller workers and performed the OTTO analysis that resulted in an uncertain $L = 186.9$. In 1987, population size had enlarged further ($A = 28$) and I detected 5 or 6 queens on nest surface in early spring but **L** was still unclear ($L = 184.6$). The first save mathematic indication for polygyny with $L = 169.7$ I got in 1988 and population size was estimated equal to the previous year. This colony had obviously performed a shift from monogyny to polygyny in 1985 and possibly I would have got an $L > 188$ in case of calculation in late summer of this year and thus a misidentification.

Nest No 309, formerly a very populous **pht p** colony with a mound of 360 cm diameter and 120 cm height, is another example for a possible misidentification. No 309 was dying out in 1988. There were only a few hundred, mostly large surviving workers on the mound for which I calculated $L = 197.9$ which would definitely mean monogyny. A queen was not found and I believe the skewed distribution towards large workers more likely to be the result of the higher life expectancy of larger workers rather than to be an expression of a longer period of monogyny.

In very small colonies with small workers the OTTO function is suspected to provide, in case of bad nutritional conditions, an erroneous indication for polygyny but I have still no evidence for such a type of misidentification.

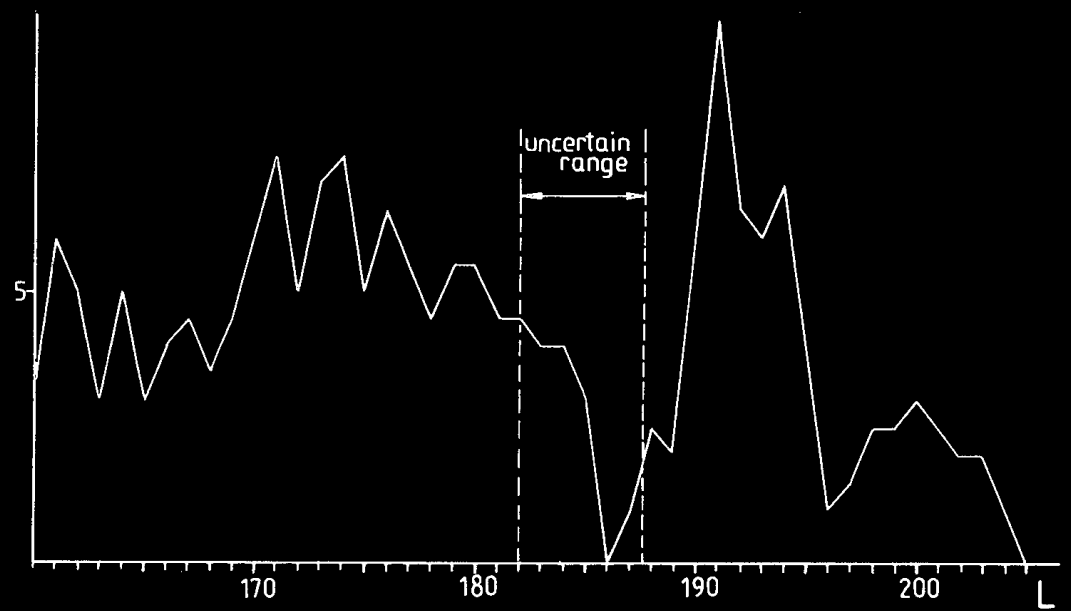

Fig. 13 The OTTO discriminant **L** to distinguish between monogyneous and polygyneous nests. Shown is only the interval **L** [160, 205]

5.2. The frequency of monogyny and polygyny in the phenotypes and the associated ecological strategies

We observe highly significant differences between the phenotypes in the frequency of monogyny polygyny. In **pht P**, 4 nests (= 2.4 %) were monogyneous and 160 polygyneous. OTTO (1960) reported for *Formica polyctena* from a sample of 59 investigated nests 5.1 % as monogyneous. It is likely that OTTO's *"Formica polyctena"* included a certain fraction of **pht I** nests which could explain the higher monogyny frequency. In **pht I**, I found 10 **pht I^M** nests (= 14.3 %) and 60 **pht I^P** nests which is, if tested in a χ^2 test, a highly significant difference ($p < 0.005$) to **pht P**. Still much larger is the difference to **pht R** where we have 148 **pht R^M** nests (= 75.9 %) and 47 **pht R^P** nests. Such a decrease of monogyny frequency from **pht R** across **pht I** to **pht P** (75.9 % – 14.3 % – 2.4 %) has many functional implications regarding the ecological strategy.

In general, it is an advantage for the fitness of a species to maintain in its gene pool a morphological and behavioural polymorphism. A reduction of polymorphism, i. e. the clear preference of a single ecological strategy is allowed when the habitat provides required recource states in high and stable quantities for many generations. However, the conditions may change in such environments and the fitness of a species will be higher on the long-term scale if the gene pool has maintained at least in a small portion an alternative strategy. Such an ecotype is very probably presented by **pht P** for which I estimate to found at least 95 % of new nests by colony splitting and 5 % or less by socialparasitic colony intiation after dispersal flight. Such a socialparasitic colony foundation is very evident in nest No 106. This **pht P^M** nest was discovered in a small wood isle within a large area of arable land near Luckau. In the site were present no other nests of any phenotype, no traces of abandoned older mounds could be found, and the potential host species *F. fusca* and *F. cunicularia* were abundant.

In coherent, large woodland areas, the favoured strategy for **pht P** is to extend its range through "step-by-step" dispersal by colony fission and to make a "lage-scale-conquest" (ROSENGREN & PAMILO 1983) getting a superior place in the dominance hierarchy of insect societies. However, for eventual dispersal across large areas of land with no suited habitats, it must be very advantageous to maintain at least in a small portion the behavioural repertoire of single queen dispersal flight. Once having founded the first colony in such a way on a distant habitat patch, there is the chance to shift to polygyny and then to build up a polycalic colony. Such a sequence of events I assume for the site Petschkenberg – a small wood islet of 5000 m² in a vast area of bare arable land and 1.5 km away from the nearest small forest – where a polycalic colony of five large

pht P nests was established which dominated this small habitat patch completely. However such observations were rare in **pht P** for which we may assume a low dispersal flight tendency.

A very different ecological strategy we may expect for **pht R** concluded alone from the inverse monogyny polygyny ratio. To prove this hypothesis, a special investigation of 22 wood islets, each not larger than 1.5 ha and completely isolated from other woodland by bare 0.3–1.5 km broad areas of ploughed land, was performed in the eastern Oberlausitz. A colonization of these small wood patches by colony fission and well-directed walking of the split-off population across a large "desert area" to hit finally a very small target seems impossible and we may expect a new colonization by single queen dispersal only. However, wood ant nests existing in these small areas may have survived from ancient times when we had interconnected habitat systems and therefore the historical development needs consideration. Concluded from tree age, it seems that many of these small patches, which were peasant property, were cut during or after the Second World War in the years 1943–47 to have urgently needed firewood. These cuttings meant probably an impact on previously existing wood ant populations. So I believe that the majority of wood ant nests present now are new foundations by dispersal flight and temporary social parasitism during the last 40 years.

A comparson of these small isolated sites, having an average area of 4000 m^2, with sites in large compact forests or in connected systems of smaller woodlands is given in Table 3. As "sites" were defined in latter case arbitrarily chosen areas of 500–1500 m diameter, then a large compact forest could be subdivided into many sites although natural or man-made borders were not visible. This subjective component will probably affect the results but not disguise principal chorological facts.

The data confirm the hypothesis of reduced flight dispersal capacity to isolated patches in **pht P.** While we have no significant difference of site frequency between **pht P** and **pht R** in connected or large, compact systems, **pht P** has a significantly lower site frequency for small isolated patches ($p < 0.05$, χ^2 test). The site frequency of **pht P** in isolated patches is only 23 % of its site frequency in connected systems whereas the frequency drop in **pht R** goes to 68 % only suggesting a three times higher capacity to reach isolated patches.

A little surprising is the rarity of **pht I** in isolated patches. The frequency drop goes down to 23 % indicating a similarly reduced flight dispersal capacity as in **pht P** although the monogyny ratio is significantly higher in **pht I.** A possible explanation could be that the isolated patch site frequency is not governed alone by the colonizing potency but additionally by the potency to hold a patch or, which is very important in this context, by the chance to generate **pht I** *de novo* through hybridisation of **pht P** with **pht R.** According to the SCHOENER formula, the site overlap of **pht P** and **pht R** was only 0.08 for isolated patches but 0.367 for connected systems indicating a very different probability for possible crossbreeding.

Table 3 Occurrence of *Formica rufa* complex phenotypes in small isolated wood patches of 0.4 ha average area and in large, coherent woodland systems of the eastern Oberlausitz.

	small isolated patches	connected or compact systems
number of sites investigated	22	117
number of sites with **pht P**	3 (= 13.6 %)	69 (= 59.0 %)
number of sites without **pht P**	19 (= 86.4 %)	48 (= 41.0 %)
number of sites with **pht I**	1 (= 4.5 %)	23 (= 19.7 %)
number of sites without **pht I**	21 (= 95.5 %)	94 (= 80.3 %)
number of sites with **pht R**	10 (= 45.5 %)	78 (= 66.7 %)
number of sites without **pht R**	12 (= 54.5 %)	39 (= 33.3 %)
mean density of all phenotypes	3.28 nests ha	0.05 nests ha (rough estimate)

6. Chorological arguments for hybrid nature of phenotype I

I have performed a realistic large-area census of wood ant nest densities for very few sites only which makes impossible a reliable statistical test of the hypothesis on a close correlation between the occurrence of **pht I** and the syntopic occurrence of both putative parent phenotypes **pht P** and **pht R.** However, a rather simple consideration may show us that there seems to be in fact such a clear chorological correlation. For the same geographic region considered here, OTTO (1968) reported a mean density of 5.8 wood ant nests 100 ha woodland area calculated from 15.500 test squares of 2500 m^2. This test-square method is surely a representative census though underrecording of very small nests by the foresters seems possible. Subtracting the *F. pratensis* complex members, I calculated from OTTO's data an approximate spacious density of 4.7 nests 100 ha for the *F. rufa* complex phenotypes. Since we have indications for a decline of wood ant populations in East Germany during the last 20 years, it is surely no underestimation to speak for the present time of a spacious density of 5.0 nests 100 ha woodland area. If we assumed a mean abundance of 2.5 **pht P** nests and 2.0 **pht R** nests 100 ha and an ideally homogeneous distribution, an area of 50 ha were necessary to hold both putative parent phenotypes with at least one nest each. 15 sites with **pht I** nests were searched for **pht P** and **pht R** nests within a radius of 200 m (or an area of 12.6 ha). In 11 of these **pht I** sites *both* putative parent phenotypes were present within the search area of 12.6 ha and in 4 sites they could not be found together. For conditions of a homogenous distribution, we would predict 3.78 of these search plots to hold both **pht P** and **pht R.** The observed and predicted frequencies 11 : 3.78 and 4 : 11.22 are significantly different with $p < 0.001$ in a χ^2 test after FISHER & YATES which is in my opinion a clear indication for a dependency of occurrence of **pht I** from enlarged densities and syntopic occurrence of parent phenotypes as it must be demanded to facilitate crossbreeding.

Another argument for putative hybrid identity provides the interesting geographical distribution of **pht I** in East Germany. In the Oberlausitz, south of the line Bischofswerda–Bautzen–Niesky, as much as 27.4 % from a total of 212 nests were **pht I** but I found only 6.6 % **pht I** within a total of 218 nests in the remaining part of East Germany. The latter ratio is probably typical for most parts of Central Europe meaning a rather good reproductive isolation between **pht P** and **pht R.** This is probably the main reason why the problem was not recognized by wood ant taxonomists of the past; the few intermediate samples did not bother them very much and the traditional *polyctena rufa* thought pattern was not attacked.

What could be the reason for the outstanding abundance of **pht I** in the mentioned part of the Oberlausitz? The map of this region shows characteristically a very chaotic, "coarse-grained" woodland distribution. Large and compact woodland systems as in the northern Oberlausitz, in Mecklenburg, the Mark Brandenburg, the Thüringer Wald, the Erzgebirge or the Harz are rare in this interesting area but in general we have no lack of woodland. There are many forests but the majority of them has an area between 0.5 and 10 km^2 and locally we have dense wood ant populations. If we assumed **pht P** and **pht R** were species in the making, they should have developed certain isolating factors and they should tend to a niche segregation reducing the probability of encounters. Exactly this isolating niche segregation is more likely in landscapes with a more compact woodland structure. Here, **pht P** will preferentially perform its "large-scale conquest" strategy and **pht R** will preferentially follow a "long-range-dispersal" and "quick colonizing" strategy. The first strategy tends to make dispersal allover the *area* of a forest by colony splitting while the latter will perform a linear dispersal *along margin lines* of the forest where host nests for socialparasitic colony foundation are abundant. This refers to external and internal margin lines but in compact forests internal margins are rare. These differing distributional strategies will produce a certain degree of sympatric spatial segregation and will decrease together with other isolating factors the probability for hybridisation in landscapes with compact woodland. This sympatric spatial segregation should be weakened the more a region has a torn, chaotic woodland structure in which we have a much higher ratio of margin line length against area. Such a condition plus sufficiently dense populations of **pht P** and **pht R** will increase the probability for hybridisation and this was most likely the process responsible for extraordinary high abundance of **pht I** in a special part of the Oberlausitz (for a more detailed discussion see section 10).

7. Allochronic nuptial flight and separate mating places as possible factors isolating phenotypes P and R

The isolating factors explained above are probably enhanced by a partial segregation of mating time and mating place in **pht P** and **pht R**. DLUSSKY (1967) reported that the swarming periods of *F. polyctena* (= **pht P**) and *F. rufa* (= **pht R**) were frequently allochronic in the same lacality, altough there was much overlap if larger territories were considered. I have not observed many flights directly. However, concluded from time of appearance of alates on nest surface, flights of **pht P^P** should be on average earlier than in **pht R^M** of the same locality which confirms DLUSSKY's statements. This temporal segregation is surely not perfect but a certain contribution to reproductive isolation is expected. The main reason for this allochrony could be the much larger average population size in **pht P^P** nests allowing a faster brood development by intranidal heat production in early spring.

Another factor enhancing isolation is very probably an average difference in mating places. Males of **pht P^P** showed an excessive copulation behaviour already on mound surface; in nests without queens they tried to mount workers or even individuals of own sex. If **pht P^P** alates left the nest area, I had the impression that the flights were short-ranged. Copulations were seen in close vicinity of the nest, on ground or on bushes. In contrast, I could not observe copulation behaviour in **pht R^M** alates on mound surface or near the nest. They showed an elevating flight after leaving the mound and quickly disappeared for the human eye. Very likely there are different orientation mechanisms guiding alates of **pht P^P** and **pht R^M** which reduce the mating place overlap.

In case of direct encounter of **pht P** and **pht R** alates during swarming, there is obviously no principal mechanism to prevent a mating and successful insemination: GÖSSWALD & SCHMIDT (1960) observed *"F. polyctena"* and *"F. rufa"* to copulate freely and got developing broods of F_1 generation in laboratory experiments. Unfortunately this F_1 generation was not reared up to imaginal state because the laboratory nests were infested with parasitic mites.

8. The influence of size and type of nest populations on worker body size

It is common use among Central European wood ant observers to obtain an approximate reflection of nest population size by estimation of the outer diameter **d** of the nest area which is defined by the position of the most peripheral nest entrances. In nests with a conspicous surrounding belt of soil ejections, as typical for medium-sized to large polygyneous nests, these most peripheral entrances are normally located near the outer margin of the ejection zone. In nests with no or weak ejections, as frequently seen in monogyneous or newly founded polygyneous nests, these entrances are normally located very near to the margin of mound base.

However, an estimation of population size from outer diameter **d** has several sources of error. To name one of the most important errors, monogyneous colonies of all phenotypes have a clearly lower ratio of population size against basal area than polygyneous nests. Often we observe in monogyneous nests rather large mounds made with coarse plant materials but inhabited by a rather small population which is sometimes no longer able to guarantee a complete turnover of mound material. As a consequence, the base of such mounds is often being in decomposition and the actual population is confined to the top of mound which is constructed larger and larger throughout the years but the worker number does not grow proportionally.

To avoid this kind of error, I have tried to make an assessment of nest population by estimation of the surface area covered by ants. If, for instance, the nest surface area within outer diameter **d** was calculated as 300 dm^2 and I estimated 20 % of this area to be covered with ants, a "population size figure" **A** of 60 dm^2 could be derived. The value A gives on average a better reflection of the real population size but is heavily dependent from temperatures and seasonal effects which strongly influence activity and distribution of ants. In this context, it should be noted that the depression of ant coverage of the nest surface caused by direct solar insolation on hot summer noon may be much stronger than a depression by very low temperatures. To minimize these errors, estimates of **A** were

performed only in the period from late April to late September at air temperatures at the nest site between 15° C and 22° C.

The regressions of population size figure **A** against outer nest diameter **d** were surprisingly different in polygyneous and monogyneous nests of all phenotypes. For polygyneous nests I got

$$A = 0.0024\ d^{1.867} \qquad (r = 0.8648,\ n = 132,\ p < 0.0001)$$

and for monogyneous nests

$$A = 0.00888\ d^{1.386} \qquad (r = 0.6082,\ n = 91,\ p < 0.0001).$$

These functions confirm the above statement that monogyneous nests have for equal **d** a distinctly lower population size. One possible explanation for this difference gives the higher physical strength of workers in monogyneous nests which use significantly larger particles for mound construction and show a behavioural trend to build up steeper mounds.

The largest nest of **pht P** (nest No 227) I found in East Germany had a basal area of 23.8 m^2 and an estimated A of 550 dm^2. A **pht P** nest still larger was shown me by G. Dlussky at Svenigorod Moscow District in 1985. A measuring of this giant nest was not performed but I estimated the mound alone to have 6 by 8 meters basal diameter (or at least 39 m^2 basal area) and a height of 1.5 meters. An attempt of Dlussky and Zacharov (Dlussky, pers. comm.) to estimate the population number of this nest resulted in 15 million individuals. The walking movements of the workers produced a noise well perceptable by the human ear still 30 meters away from the nest.

		pht P^P	pht P^M	pht I^P	pht I^M	pht R^P	pht R^M
HW	mean	1576	1794	1646	1793	1639	1817
[µm]	SD	102	48	79	61	63	77
	n	18	3	22	8	25	27
d	mean	204	70	140	94	98	92
[cm]	SD	122	28	74	36	50	41
	n	93	2	42	7	29	101
	maximum	550	90	300	120	250	200
A	mean	71.5	7.8	31.0	5.79	16.4	5.65
[dm^2]	SD	89.2	8.2	27.1	2.25	14.6	3.77
	n	101	2	44	8	29	111
	maximum	550	13.5	111	8.1	61.6	19.1

Table 4 Nest means **HW** of worker head width, outer nest diameter **d**, and population size figure **A** of polygyneous and monogyneous nests of all phenotypes. The **HW** were taken from the 103 representative samples from which the discriminant **L** was computed (see 5.1) with a total of 7000 workers.

Regarding the head width data in Table 4, there was a certain bias in the selection of samples because very populous **pht P^P** and **pht I^P** nests with small workers where polygyny was not in question and **pht R^M** nests with very large workers where monogyny was doubtless were frequently not investigated for their head width distribution (see 5.1.). Thus the **HW** of **pht P^P** (1576 µm) and **pht I^P** (1646 µm) are probably a little larger and those of **pht R^M** (1817 µm) somewhat smaller than in case of unbiased sample selection. The **HW** of phenotypes P^P, I^P and R^P are very similar but the mean of **pht P^P** is significantly ($p < 0.05$) smaller than the means of I^P and R^P which is doubtless a function of the much larger average population size in **pht P^P**. In polygyneous nests, a growing population size is expected to be correlated with a decreasing worker queen ratio and thus correlated with decreasing food supply of worker larvae, particulary with a shortage of growth-stimulating secretions of labial and maxillary glands (see OTTO 1962, LANGE 1954). In monogyneous nests, a growing population size means selfevidently an increasing worker queen ratio and consequently the above theory will predict an increase of average worker size. The following regressions show in fact for monogyneous nests positive and for polygyneous nest negative correlations between population size **A** and mean head width **HW**. For **pht P^P** was calculated

$$HW = 1640\ e^{-0.000469\ A} \qquad (r = -0.8794,\ n = 15,\ p < 0.001).$$

For **pht I^P** and **pht R^P** were calculated similar trends but the regressions were not significant in both cases. A pooled regression of phenotypes **P^P**, **I^P** and **R^P** gave

$$HW = 1653\ e^{-0.0004734\ A} \qquad (r = -0.6186,\ n = 53,\ p < 0.001).$$

For **pht R^M** was calculated a relation

$$HW = 7.471\ A + 1769 \qquad (r = 0.4535,\ n = 24,\ p < 0.05).$$

For **pht I^M** and **pht P^M** I had an insufficient number of data but a pooled regression of **pht P^M**, **pht I^M** and **pht R^M** resulted in

$$HW = 7.408\ A + 1767 \qquad (r = 0.4243,\ n = 30,\ p < 0.05).$$

The data in Table 4 show that **pht I** is an intermediate also in population size. After a $A^{0.4}$ transformation of **A** data to approximale normal distributions, a t test proved highly significant ($p < 0.001$) differences between the means of **pht P^P**, **pht I^P** and **pht R^P** in each possible comparison.

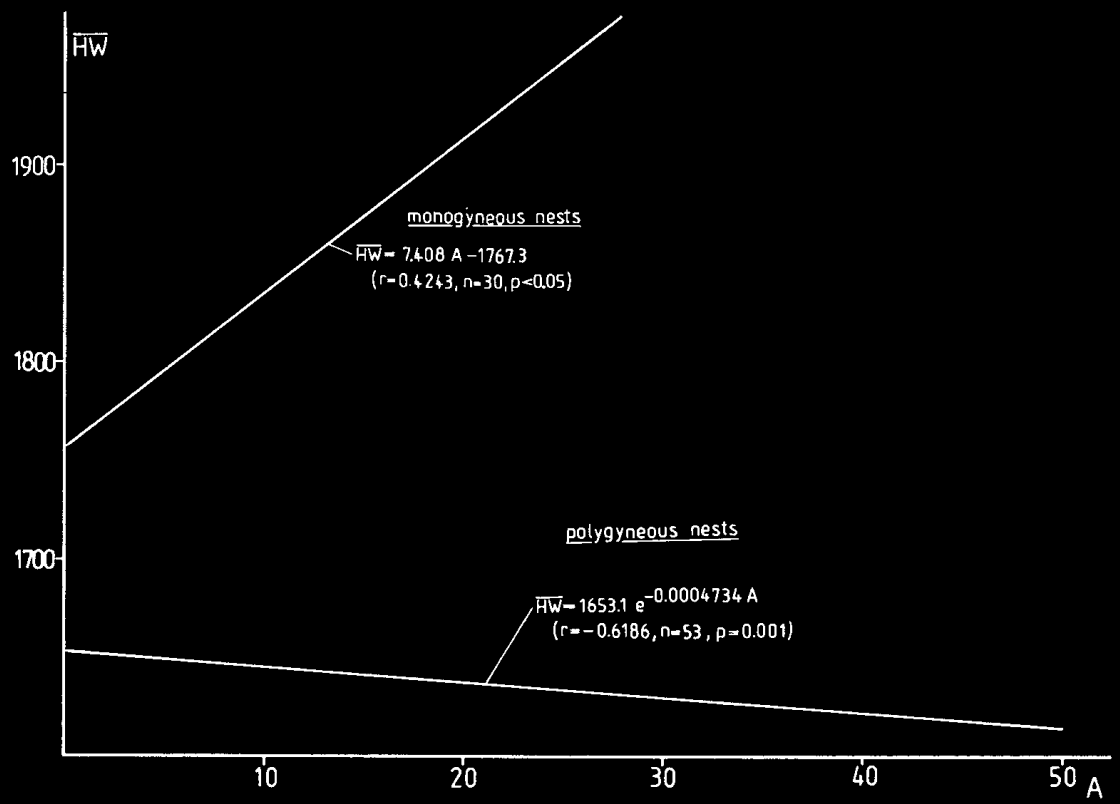

Fig. 14 Dependency of mean head width **HW** of worker nest samples of 50—100 specimens per nest from population size figure **A**

9. The occurrence of epizoic fungi

There is evidence that epizoic fungi have increased their abundance in Central Europe during the last two decades (WISNIEWSKI 1976, 1977; ESPADALER & WISNIEWSKI 1987). In my material, as much as 12.6 % of 430 nests were infested which a grees well with WISNIEWSKI's data for the adjacent areas of W and SW Poland from where he reported 10–16 % of wood ant nests as host of *Aegeritella superficialis* BALAZY et. WISNIEWSKI, 1974. What I have called here "epizoic fungi" probably refers in the majority of cases to this deuteromycete species but others as *Erynia mymecophaga* (TURIAN et. WUEST) may be expected in lower frequencies according to the references above. OTTO, who intensively investigated wood ants in East Germany during the years 1955–1967, did not

mention epizoic fungi in his many publications and thus it seems likely that these fungi were much less abundant in this time.

Table 5 shows the frequency of infestion with epizoic fungi. A χ^2 test proves highly significant ($p < 0.001$) differences in the ratio of infested nests in comparisons of **pht P** / **pht R** and **pht I** / **pht R**. Significantly differ the fungus frequencies between **pht P^P** and **pht R^P** ($p < 0.01$). A pooled comparison of polygyneous nests of all phenotypes (19.1 % infested nests from a total of 267 nests) with monogyneous nests (1.85 % from a total of 162 nests) show a highly significant difference ($p < 0.001$).

	pht P^P	pht P^M	pht I^P	pht I^M	pht R^P	pht R^M
number of nests investigated	160	4	60	10	47	148
number of nests with epizoic fungi	38	0	11	0	2	3
ratio of nests with epizoic fungi	23.8 %	0 %	18.3 %	0 %	4.3 %	2.0 %

	pht P	pht I	pht R
number of sites	72	25	88
number of sites with fungi	29	6	5
ratio of sites with fungi	40.3 %	24.3 %	5.7 %

Table 5 Frequency of infestion of *Formica rufa* complex phenotypes with epizoic fungi.

Also of interest is the percentage of infested workers within the same nest. The infestion ratios were 0.265 ± 0.256 (range: 0.05 — 0.96) in 29 infested nests of **pht P**, 0.192 ± 0.164 (range: 0.05 — 0.70) in 11 infested nests of **pht I**, and 0.307 ± 0.268 (range: 0.05 — 0.60) in 4 infested nests of **pht R**. These are insignificant differences in each possible comparison.

These intranidal infestion rates and the data of Table 5 strongly suggest the observed differences to be the result of differing colony structure and colony foundation modes. The hypothesis different biochemical properties of cuticular surface (fungicide growth inhibition, nutritional growth limitation) were responsible for between-phenotype differences seems much less probable. Once a nest was infested, the deuteromycete distributed among the worker population with similar frequencies in each phenotype.

I can not remember that one of the 200–300 queens investigated with the microscope ever carried a fungus. If at all, then queens are undoubtedly much less infested than workers. An explanation could be the very intensive and persistent cleaning and licking of whole surface of the queens by the workers giving the fungus no chance for bulbil initiation. As a consequence, a single-queen nest foundation after dispersal flight will considerably reduce the infestion risk of the new colony whereas foundation through nest-splitting will often make the daughter nest as infested as the mother nest. This explains well the striking differences in parasitation between monogyneous and polygyneous colonies. I have seen polycalic colonies, three in **pht P** and two in **pht I**, where each nest was more or less infested. The fungi seem not to attack the ant's life directly, hyphes do not penetrate the cuticula nor damage the chitin layer. However, a negative effect is surely provided by overgrowth of sensory organs and by hindering movements in case of very heavy parasitation.

10. The proposed taxonomic designation and the concept of sympatric subspecies divergence

The exactly intermediate position of pilosity characters in **pht I** (3.1., 3.3.), the chorological arguments (6.), and the intermediate position of **pht I** in size (8.) and structure (5.2.) of nest populations strongly suggest we have an imperfect reproductive isolation between *F. rufa* **(pht R)** and *F. polyctena* **(pht P)** leading to the emergence of hybrid populations **(pht I)**. However, the demonstration of three clear morpho-ecological phenotypes indicates that we should have relatively well-developed isolating factors and a certain selection on stability of these phenotypes. If not, we would have to expect a higher frequency of unclear samples.

Obviously we have here a borderline case of taxonomic interpretation difficult to treat with binary nomenclature. On the other hand, a strict application of binary nomenclature would produce conflicts for practical students of wood ants:

(i) To speak only of *Formica rufa* would ignore the fact that we have entities with very different biological parameters and that the designation of these entities is highly desired in the context of ecological studies and wood ant protection and

(ii) to make up three good species would ignore all what was reported in this paper.

Thus it seems the most appropriate taxonomic treatment to regard **pht R** and **pht P** as relatively stable sympatric subspecies or ecological races of *Formica rufa* with the taxonomic designation *Formica rufa rufa* Linnaeus 1761 **(pht R)** and *Formica rufa polyctena* Förster, 1850 **(pht P).** As taxonomic designation for the hybrid **pht I,** I propose *F. r. rufa* x *polyctena.*

As a consequence, I plead for the moderate and cautious(!) reintroduction of sympatric subspecies concepts if there is enough evidence to justify such an interpretation as in the presented case. This must not mean a return to the destructive FOREL concept to name arbitrarily hybrids and to produce a great number of subspecific and infrasubspecific names.

Sympatric and parapatric speciation have very likely a great importance in speciation of insects, a sympatric speciation particularly in the parasitic species groups (ZWÖLFER & BUSH 1984, ENDLER 1977). For non-parasitic species a complete sympatric speciation is not probable but at least a trend to divergence is expected under certain conditions. The wood ants considered here are in part non-parasitic (those which spread by colony fission) and in part temporary parasites (those founding new colonies as single queens). A trend for segregation into the sympatric subspecies *F.r. rufa* and *F. r. polyctena* can be predicted if we postulate a model of two genes the first of which determines the mating place and the second modifies the action of the first and determines the mode of colony foundation. The model makes following basic assumptions:

(i) We have a large compact woodland with low ratio of margin line length against area.

(ii) *Serviformica* nests as host nests for socialparasitic colony foundation are abundant at the margins but very rare inside the woodland.

(iii) The first gene with dominant allel **A** and recessive allel **a** directs the mating place orientation with genotypes meaning

AA and **Aa**: long-range mating flight towards margin structures

aa: mating near the nest, no longe-range flight to margin

(iv) The second gene with dominant allel **B** and recessive allel **b** modifies the action of the first gene and directs the mode of colony foundation with genotypes meaning

BB and **Bb**: high potency for socialparasitic colony foundation, no inhibition of long-range mating flight (**AA** and **Aa**)

bb: very low potency for socialparasitic colony foundation, colony foundation by nest-splitting, inhibition of long-range mating flight (**AA** and **Aa**)

As best coadaption for the inner woodland area is predicted genotype **aabb** which could be represented by **pht PP** (or the typical *polyctena)* and as best coadaptions for the margin lines genotypes **AABB, AaBB, AABb** and **AaBb** which could be represented by **pht R^{M}** (or monogyneous *rufa*). The genotypes **aaBB, aaBb, Aabb,** and **AAbb** would have a reduced fitness inside the woodland and on the margin as well and should be counterselected.

Such a model can not explain a complete segregation of genotypes since a certain gene flow between the inner woodland and margin population is always given. However, a clear trend to increase the frequency of the best coadapted homozygous combinations **aabb** for the inner woodland and **AABB** for the margin habitat is predicted in case of large compact woodland systems where the probability for contacts of both genotypes is lower. In such areas, *F. r. rufa* and *F. r. polyctena* appear as rather well separated sympatric subspecies the more we have here a higher probability for allochronic nuptial flights.

The high local abundance of the hybrid *F. r. rufa* x *polyctena* in landscapes with a torn, "coarse-grained" woodland structure (27 % of all nests in a certain part of the Oberlausitz) indicates that it should have a high fitness and raises the question which kind of selection could stabilize the hybrid population. I have got the impression that the hybrid tends to a more often shift of nest sites than *F. r. polyctena* and seems to be less sensitive to some drastic effects of management. Additionally its higher tendency for monogyny is surely an advantage in regions with coarse-grained woodland structure where the combination of two principal ecological strategies will very probably make the hybrid more plastic than *F. r. polyctena.*

11. Summary

432 wood ant nests of the *Formica rufa* complex (the phenotypes near to *rufa* L. and *polyctena* Förster) were investigated in the territory of East Germany for their pilosity characters, population size, monogyny frequency, and other characters. On the basis of nest samples containing 7–20 workers per nest, 8 pilosity characters and head width were investigated by a standardized method giving a total of 55 000 primary data on morphology. Three clear phenotypes **pht P, pht I,** and **pht R** could be demonstrated. On the basis of sample means, it was possible to determine 427 nests (= 98.8 %) to belong to one of the three phenotypes. The influence of body size on pilosity data can be neglected in distinction between **pht P** and **pht I** but is important for decisions between **pht I** and **pht R.** The intermediate **pht I** is interpreted as fertile hybrid between the sympatric subspecies *Formica rufa polyctena* (**pht P**) and *Formica rufa rufa* (pht R). This was concluded from the exactly intermediate position of the mean values of the 8 pilosity characters, from the fact that the hybrid was much more abundant in sites where both parent entities were in close neighbourhood, from the intermediate frequency of monogyny and the intermediate size of polygyneous nests. The hybrid **pht I** is further characterized by a striking breakdown of correlations between the pilosity characters (0.18 compared to 0.49 in **pht P** and 0.51 in **pht R**). Two examples for nests with very obvious phenotype mixtures (**pht I + pht R**) and two other examples for shifts from one phenotype to another (**pht P** to **pht R**) are reported. Nest samples are necessary to enable a safe distinction between queens of all three phenotypes. The method of OTTO (1960) is confirmed as most useful to distinguish between monogyneous and polygyneous nests and possible sources of error are considered. The ecological strategies associated with monogyny and polygyny are discussed. The monogyny frequencies increase from **pht P** (2.4 %) across **pht I** (14.3 %) to **pht R** (75.9 %). Evidence is presented that the mean worker body size increases with growing population size im monogyneous nests but decreases with growing nest population in polygyneous nests. The average differences between the phenotypes in frequency of infestion with epizoic fungi (**pht P** 23.2 %, **pht I** 15.7 %, **pht R** 2.6 %) are explained by the differing colony structures and modes of distribution and not by differing biochemical properties of cuticular surface. The hybrid **pht I** is extraordinary abundant (27.4 % of 212 nests) in a region of the Oberlausitz with a torn, coarse-grained woodland structure whereas it is rare (6.6 % of 218 nests) in regions with large, compact woodland systems having a low ratio of margin line length against area. A model of sympatric subspecies divergence is proposed which may explain the low frequency of hybrid populations in regions with compact woodland systems and their high frequency in torn coarse-grained systems. As taxonomic designations are proposed *Formica rufa rufa* Linnaeus, 1761 **(pht R),** *F. rufa polyctena* Förster, 1850 **(pht P)** and *F. r. rufa* x *polyctena* **(pht I).** The low freqency of doubtful samples indicates that there should exist a selection on stability of the hybrid population.

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